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Some essential physiological characters of soil invertebrates

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Summary :

Conditions of gas exchange and water balance in the soil are intermediate between aquatic and aerial ones : in the soil there exists the possibility of air breathing practically without loss of water. In particular this enables soil animals to skin respiration though the use of elaborated aerial respiratory organs is also effective. Ecological and physiological properties of soil animals are different in various dimensional groups. The smallest forms (Protozoa, Rotatoria, Nematodes, etc.) are connected with the liquid phase of the soil and physiologically are very similar to aquatic ones.

Smallest arthropods (Acari, springtails, etc.) are inhabiting air filled small holes in the soil and are hygrophilous air breathing organisms avoiding direct contacts with water films. Really connected with the soil as whole larger invertebrates are (earthworms, holometabolous insect larvae, etc.) They have special adaptations to the locomotion in the soil, normally air breathing, but being in contacts with the liquid phase of the soil have many properties common to aquatic animals. Thus insect larvae can have permeable skin enabling cutaneous respiration, being poikilosmotic, able to saprophagy, orientating after the concentration of soluble matters, tolerating high CO_2 concentration, realizing vertical migrations, etc. Many holometabolous soil insect larvae being typically air breathing reveal characters intermediate between aquatic and epigean dwellers.

Key words : soil, soil invertebrates, adaptation.

The majority of ecologists discriminates only two main environments of free living (non parasitic) animals – aquatic and terrestrial ones (CLARKE, 1954; HESSE, 1924; etc.). To these two environments soil zoologists, soil ecologists added during the last 30-40 years a still one special environment — the soil, which drew the attention of Ch. DARWIN, what is to mention this year, year of DARWIN's death centenary.

Peculiarity of the soil as an environment depends on the fact that it presents a complicate three-phase polydisperse system. It includes solid particles of various size from larger sand to colloid ones which form aggregates of various complicity : the interstices between solid particles are filled with air and water; voluminal ratio of liquid and gaseous phases is different in soils of various types, in various zones and seasons, depending on weather conditions. The liquid phase — soil water may be in various states — hygroscopic, filmy (firmly or loosely connected with solid particles) capillary and gravitational. When the soil contains the amount of water twice higher than the hygroscopic one, the soil air is saturated with water vapour. Therefore the loss of water by soil organisms due to the transpiration is negligible even at small depth.

The principal vital differences in animal existence in water and on land are differences in respiration conditions and the danger of desiccation on land in the open air. The content of the oxygen in the atmosphere air is much higher than there is dissolved in water : therefore the difficulty of transition of aquatic organisms to the aerial respiration is due principally to the desiccation of respiratory surfaces in the air.

Gas exchange in organs of aquatic respiration, especially in skin breathing animals, can proceed in the air saturated with water vapour. Transition of aquatic animals with not high differentiation of respiratory organs to the air breathing, especially in skin respiring invertebrates, is possible through the environment where the air is water vapour saturated. Such a medium provides the possibility of air breathing with the minimal loss of water. Such an environment is represented by the soil (litter is regarded as the uppermost layer of the soil) and similar (according to the ecological characteristics) habitats – cracks in rocks, plant debris, cavities under stones, etc. (GHILAROV, 1949). The totality of such habitats was later called « porosphere » by VANNIER (1973) who has repeated all my arguments concerning the originality of life conditions in this environment.

In the course of phylogeneses by the transition of aquatic groups of animals to the terrestrial life the conditions of soil habitat were broadly used. Recently among free living (non-parasitic) terrestrial *sensu lato* (non aquatic) groups of animals inferior ones are soil animals or closely connected with the soil and similar habitats revealing many characters of physiological similarity with water dwellers. Representatives of aquatic groups leaving life in waterbodies also become soil inhabitants.

The main physiological similarity between soil and water animals is the permeability of teguments enabling the possibility of gas exchange both in water and in the damp air. Among soil dwellers — invertebrates — it is possible to discriminate three principal dimensional groups, for each of them the soil represents different environment. Microscopic animals — protozoans, rotifers, etc. — are physiologically aquatic animals, their immediate environment is not the soil as a whole but concentrations of liquid water in various forms. Microarthropods are inhabitants of air-filled interstices, cracks and passage-ways in soil, they are typically air-breathing animals requiring the high humidity of the air.

Larger soil invertebrates — earthworms, geophilids, larvae of insect etc. — are air-respiring animals whose whole body surface is immediately contacting with all phases of the soil.

Representatives of all these groups as well consuming oxygen dissolved in water as air-breathing ones are characterized by their ability to the skin respiration.

Soil turbellarians, nemertines, oligochaetes are characterized by skin respiration; their body surface is moistened with slime glands secretion. Skin respiration is also characteristic of small invertebrates having a non-chitinous cuticle (nematodes, rotifers, tardigrades, etc.).

Small arthropods with chitinous cuticle (mites, symphilids, tracheaeless proturans and collembolans) are also skin respiring, their tegument is permeable for the gas exchange without moistening of the surface.

Many bigger soil arthropods, possessing tracheal system, are able to skin respiration too. Sometimes the tracheal system in juvenils of the first instar is wanting developing but later, as in geophilid centipedes. In some spiracleless insect larvae gas exchange is realized through the skin only (some mycetophilids, *Smittia*, etc.). In many soil mites, centipedes, Apterygota, larvae of Endopterygota a significant part of the tegument surface is deprived of the epicuticle and the respiration is realized through the skin.

I have experimentally proved (GHILAROV, 1947) on the example of *Tipula paludosa* that in this crane-fly larva the rate of skin respiration (oxygen uptake, stigmata being switched off) varied in limits 35-106 % of the corresponding check (normal respiration), whereas when excluding cutaneous respiration the rate of tracheal respiration only was but 22-55 % of the normal one.

The cuticle of crane-fly larva is without the microscopically differentiated lipid or wax epicuticle being only covered with microscopic epicuticular hairs.

Permeability of the tegument in soil invertebrates for the gas exchange makes them also permeable for transpiraion, this is a common character of aquatic dwellers too, provoking their rapid death from desiccation in the open air with moisture deficit. Tegument of soil invertebrates, insect larvae included, is permeable for ions also. On the example of crane-fly larvae it has been proved for radioactive cations of potassium and anions of orthophosphoric acid marked by phosphorus. Diffusion of potassium ions proceeds more rapidly than that of orthophosphate acid anions (GHILAROV & SEMENOVA, 1957). Similar results were obtained by SEMENOVA (1958) when studying the permeability of maychafer white grub cuticle. Still in 1934, SUBKLEW studied the permeability of teguments of click-beetle larvae (wireworms) of the genus *Agriotes* and found that the rate of penetration of investigated ions shows a definite series, quite analogous to corresponding series obtained on marine invertebrates, in particular on sea cucumbers (GHILAROV, 1949).

Soil animals, including larvae of Endopterygota, are in some degree poikilosmotic, as many hydrobionts are. Among physiological properties common to soil and aquatic animals it is to mention the ability to orientation according to the gradient of dissolved matters. It was proved even on such animals as wireworms, whereas even localization of corresponding sense organs was established (LEES, 1943). This ability was the base to elaborate the control measures against these pest (PONOMARENKO & KAZADAEV, 1981).

The ability of such soil inhabitants as myriapods, Apterygota, Endopterygota larvae to emerge on the soil surface is connected with the development of impermeable for transpiration (and gas exchange) covers. At the initial stage of such an adaptation only the tergal body surface of segments is covered with the waterproof epicuticle, but with the transition to the permanent habitation in air milieu — all the body surface or its major part becomes protected by epicuticular layer.

In evolutionary aspect the differentiation of the tegument into parts impermeable for respiration and transpiration and those where the gas exchange takes place was the premise of the development of tracheal system, convergently evolving in different arthropod phyla, in Onychophora and even in land Polychaeta. For such groups as Oligochaeta, nematodes, etc. the respiration is possible both in water and in humid air. For the majority of soil arthropods possessing tracheal system the immediate contact of the body surface with liquid water is physiologically unfavourable and they have adaptations to prevent skin surface wetting. There are various hydrophobous hairs (sometimes microscopic ones), epicuticular caps as on the tops of body surface tubercules in onychiurans etc. Hydrophobous epicuticular surfaces create around the animal body films of air (plastrons), « physical gills », in periods when soil is saturated, soil cavities being filled with water. For tracheal system of soil inhabitants it is characteristic that the stigmata are open.

A specificity of the soil air is the lowered content of oxygen and high percentage of CO_2 — in warm localities in wet seasons up to 3-5 % (instead of 0.03 % in the open atmosphere).

Lower partial tension of O_2 (10 %) and higher concentration of CO_2 does not exclude the breathing of many soil animals (larvae of cockchafer, other larval insects, myriapods, earthworms (BYZOVA & PROKOP'EVA, 1969; PROKOP'EVA, 1966; etc.). Various ecological groups of earthworms are in different degree resistant to the unfavourable changes of respiration regime : deep soil dwellers are more resistant than upper soil stratum and litter dwellers (BYZOVA, 1967).

The high content of CO_2 in the soil especially near roots, determined still one physiological character of soil inhabiting phytophagous insects — the orientation after the concentration of carbon-dioxide (KLINGLER, 1958).

The vertical temperature gradient and its seasonal inversions at some depth is an ecological characteristics common to waterbodies and soil. Seasonal, daily and weather determined vertical migrations are characteristic of soil invertebrates. According to the cold resistance soil insect larvae occupy the intermediate position between water dwellers and inhabitants of suprasoil strata.

Microscopic soil animals as to their types of locomotion are similar to aquatic ones, interstitial in particular. Microarthropods with this respect are to be regarded as animals crowling and walking on solid surface. Quite peculiar are modes of locomotion of many bigger actively burrowing in the soil insect larvae (with spines at the hind body end, C-formed larvae, etc.). DUBOIS-REYMOND (1911) in his time quite erroneously referred the modes of such locomotion to the category of locomotion on the surface of solid substrate.

The humidity of soil favourable for high activity of microorganisms makes it possible for soil animals the saprophagy as a widely distributed mode of invertebrate feeding : in various soil types, in various zones saprophages represent the bulk of soil animals. This mode of feeding is common among hydrobionts but impossible in open air. Just saprophagous animals were first land conquerors among the animals and with their activity the formation of soil was connected; their activity is nowadays also one of the main factors of soil formation and fertility.

It is to be stressed that just among soil and other analogous shelter dwelling arthropods the specific mode of insemination has developed being the intermediate one between external insemination common to many aquatic animals and internal one — the only possible in air medium. This mode which I have called external-internal one (GHILAROV, 1958; etc.), explains the origin of various types of physiologically internal insemination in different groups of land arthropods.

It is quite evident that the soil represents a quite peculiar environment, which properties are in their turn determined by the summarized activity of it inhabiting organisms.

Almost 100 years ago the great founder of the modern soil science DOKOUTCHAEFF (1883) characterized the soil as the « fourth natural body » (in addition to three discriminated by the father of systematics LINNÉ — mineral, plant, animal).

Soil zoology which developed last four decades is the best proof of this statement. Peculiar physiological properties of soil animals, as well as morphological, ecological and other ones support this view-point.

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